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Maternal Origin and Migratory History of Steelhead and Rainbow Trout Captured in Rivers of the Central Valley, California

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Abstract.—Steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) in the Central Valley of California were listed as threatened under the Endangered Species Act in 1998. Unfortunately, little is known about the distribution of steelhead in the tributaries of the Sacramento–San Joaquin River system in the Central Valley or the relationship between sympatric anadromous and nonanadromous life history types. We used analysis of otolith strontium : calcium (Sr:Ca) ratios to determine maternal origin (anadromous versus nonanadromous) and migratory history (anadromous versus nonanadromous) of rainbow trout collected in Central Valley rivers between 2001 and 2007. Of the 964 otoliths examined, 224 were determined to be from the progeny of steelhead females and 740 from the progeny of nonanadromous rainbow trout females. Progeny of steelhead maternal origin were present at all of the sites sampled, but the proportion varied among sites (0.04–0.74). Based on transects of otolith Sr:Ca ratios, only five fish were confirmed to be adult steelhead. This is a conservative estimate of the distribution of adult steelhead since, due to conservation concerns, our sampling only collected a limited number of adults. The remaining 214 fish older than age 4 were not anadromous, and 16 of them were determined to be the progeny of steelhead females. Overall, these results refine our understanding of the distribution of steelhead in Central Valley rivers and confirm reports of steelhead occurrence in those rivers.

The Central Valley of California is drained by the Sacramento and San Joaquin rivers and was once home to large runs of Chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* (anadromous rainbow trout) (Yoshiyama et al. 2000). Steelhead were historically distributed throughout the Sacramento–San Joaquin River system in the Central Valley of California (Busby et al. 1996; McEwan 2001). Climate and ocean effects and reduction of spawning and rearing habitats throughout the Central Valley have resulted in declines of steelhead returning to these streams (McEwan 2001; Lindley et al. 2006) and, in 1998, steelhead populations in the Central Valley were listed as threatened under the Endangered Species Act. Despite their popularity as a sport fish and status as a threatened species, little is known about the biology, status, and life history of steelhead populations in the Central Valley (McEwan 2001). Lindley et al. (2007) recommended that to assess the risk of extinction or develop effective recovery actions for steelhead in the Central Valley, determining the distribution of steelhead and assessing the relationship between the resident and anadromous forms of *O. mykiss* is a fundamental need. Lindley et al. (2007) stressed that any quantitative assessment of population viability will be inadequate unless we understand the role that resident fish play in population maintenance and persistence of *O. mykiss* populations in the Central Valley.

Like rivers in other regions, those in the Central Valley contain both the steelhead and rainbow trout life history forms of *O. mykiss*. How these two phenotypes are related and interact is of concern to both resource managers and researchers. Foote et al. (1989) identified three possible genetic relationships between life history forms of salmonids. First, alternative life history forms are genetically isolated and represent separate reproductively isolated populations. Second, alternative life history forms are not genetically distinct. Third, alternative life history forms are genetically distinct

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within a local area but are more similar to one another than they are to their respective life history forms outside the local area. Whether sympatric life history forms are treated as single populations exhibiting polyphenism or as reproductively isolated populations has profound implications in decisions related to protection and recovery of species (Zimmerman and Reeves 2000; McEwan 2001).

In assessing the relationship between steelhead and rainbow trout, no single answer has emerged with respect to the population structure of this species. Neave (1944) first examined the relationship of steelhead and rainbow trout in the Cowichan River of British Columbia using meristic analyses and rearing–release experiments. Neave (1944) concluded that the two life history forms should be treated as different reproductively isolated populations and that migratory behavior was hereditary. Zimmerman and Reeves (2000) used otolith microchemistry and spawning surveys to examine potential reproductive isolation between steelhead and rainbow trout in the Deschutes River, Oregon. Differences in the timing of spawning and spawning locations suggested that steelhead were reproductively isolated from rainbow trout. Further, Zimmerman and Reeves (2000) used otolith microchemistry to test maternal origin of adult steelhead and rainbow trout and found that no adult steelhead were the progeny of resident female rainbow trout and no adult rainbow trout were the progeny of steelhead females. As a result, Zimmerman and Reeves (2000) concluded that the two life history forms were acting as separate biological species in the Deschutes River. Conversely, in the Babine River, British Columbia, Zimmerman and Reeves (2000) detected steelhead and rainbow trout that had a maternal origin corresponding to resident rainbow trout and steelhead, respectively. Using genetic methods, Narum et al. (2004) identified genetic divergence and reproductive isolation between steelhead and rainbow trout in the Walla Walla River, Washington. Collectively, these results suggest that the relationship of steelhead and rainbow trout varies among locations. Introductions of nonanadromous rainbow trout stocks derived from Sacramento River populations to Argentina gave rise to anadromous life history forms (Pascual et al. 2001), indicating that rainbow trout found in the Sacramento River system may contribute to steelhead populations in some circumstances. To date, however, little work exists to describe the relationship of steelhead and rainbow trout in Central Valley streams.

Analysis of otolith microchemistry provides two important tools in the study of migratory polyphenism in salmonids. First, the chemical composition of otoliths can be used to describe migration in anadromous fishes (Kalish 1990; Secor 1992; Zimmerman et al. 2003). Strontium (Sr), an element with similar binding characteristics to calcium (Ca), is substituted for calcium in the calcium carbonate matrix of otoliths at levels relative to the concentration of strontium in the environment (Kalish 1990; Zimmerman 2005). The concentration of strontium is generally greater in seawater than in freshwater. As a result, analysis of Sr:Ca ratios across the otolith of a fish can be used to describe the migratory history of that fish between freshwater and seawater (Howland et al. 2001; Zimmerman 2005). Further, comparison of Sr:Ca ratios in the primordia and freshwater growth region can be used to determine maternal origin (resident or anadromous) based on the assumption that primordia composition reflects the environment in which yolk precursors develop (in the ocean for anadromous forms) (Kalish 1990; Volk et al. 2000; Zimmerman and Reeves 2002).

Although steelhead are monitored in some Central Valley streams, such as the American and Feather rivers, in some streams of the Central Valley their occurrence has not been documented in recent years. Anecdotal evidence and reports from anglers, however, suggest that they are present in these locations. We used otolith composition to determine maternal origin (steelhead versus rainbow trout) and migratory history of rainbow trout collected from seven Central Valley rivers. From the results of maternal origin and migratory history of rainbow trout we determined the occurrence of steelhead in Central Valley rivers, the results of which will better define the distribution of steelhead, and thus aid in the development of monitoring and recovery efforts.

Methods

Otolith collection.—Otoliths were collected from wild rainbow trout and steelhead found in the presumed anadromous reaches of six Central Valley streams: the Sacramento River, Deer Creek, and the Yuba, Calaveras, Stanislaus, and Tuolumne rivers between 2001 and 2007 (Figure 1). These streams are representative of the two major river basins that are found in the Central Valley, the Sacramento and San Joaquin rivers. A few samples were also obtained from fish in the Merced and San Joaquin rivers.

Fish and otolith collection efforts concentrated on the upper anadromous reaches of most streams, specifically in the spawning and rearing areas where rainbow trout were most likely to be found. An exception to this was the San Joaquin River, where only six juvenile rainbow trout were collected from a smolt trap. Unlike the other sites, where samples were collected from the upper anadromous reaches, the smolt trap on the San Joaquin

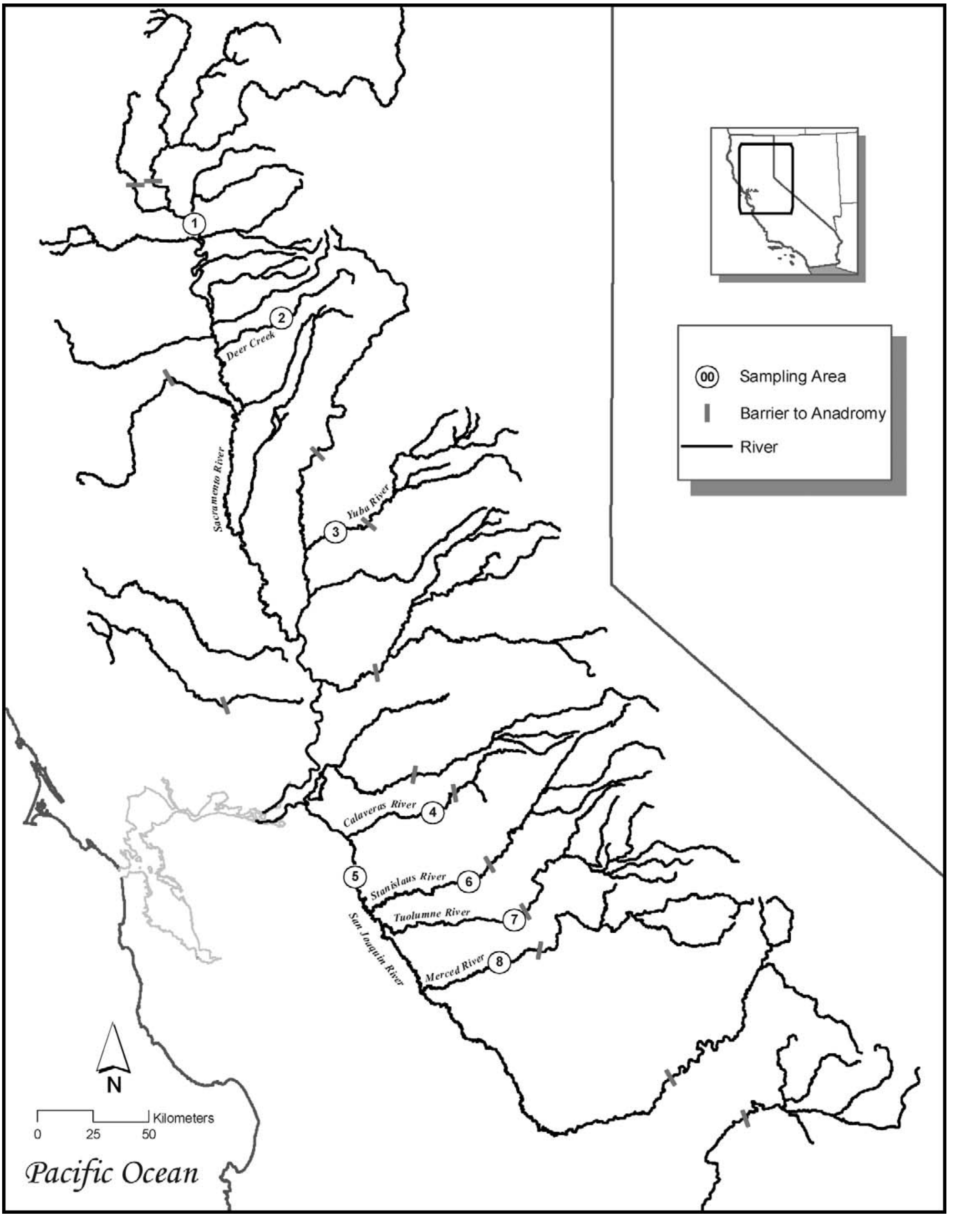

FIGURE 1.—Central Valley rivers, locations of otolith sampling, and barriers to anadromy.

River was located in the lower reach of the river and downstream from significant tributaries such as the Tuolumne, Stanislaus, and Merced rivers. Sampling was primarily conducted during the months of October through May, coinciding with steelhead migration and juvenile emigration. Sampling was limited during summer months because warm water temperatures (>21°C) could result in excessive mortality of fish during capture. Fish were captured by beach seining, rotary screw traps, electrofishing, carcass surveys, and hook and line. Fish that appeared to be sexually mature were not sacrificed for otoliths. Each fish was measured (fork length) and otoliths were removed, cleaned, and stored dry in plastic vials. Where possible, otolith samples were obtained from archives, incidental mortalities from ongoing projects, and carcass surveys in order to reduce the impact on Central Valley steelhead.

Otolith preparation and microchemical analysis.— Before preparation for chemical analyses, otoliths were immersed in water on a black background and reflected light was used to accentuate the presumed annuli. The age of each fish was determined by counting alternating translucent and opaque regions. Under reflected light, annuli correspond to the translucent zone (Kalish et al. 1995). Fish were aged and grouped by age-class as follows: young of year (age 0), age 1, age 2, age 3, and age 4 and above.

One sagittal otolith from each fish was mounted sulcus side down with Crystalbond 509 on a microscope cover slip attached on one edge to a standard microscope slide. The otolith was ground with 2000-grit sandpaper in the sagittal plane to the level of the nucleus. The mounting medium was heated and the otolith turned sulcus side up. The otolith was then ground with 2000-grit sandpaper in the sagittal plane to the level of the primordia and polished with a slurry of 0.05-μm alumina paste. The cover slip was then cut with a scribe so that several prepared otoliths could be mounted on a petrographic slide for chemical analyses.

Two methods of analysis were used to determine the chemical composition of the otoliths. First, a wavelength-dispersive electron microprobe was used to determine maternal origin of each fish following the methods of Zimmerman and Reeves (2000, 2002) and Zimmerman and Nielsen (2003). Before analysis, slides and otoliths were carbon coated. A 15-kV, 50-nA, 10-μm-diameter beam was used for these analyses. Strontiantite and calcite were used as standards for Sr and Ca, respectively. The two elements were analyzed simultaneously and a counting time of 40 s was used to maximize precision (Toole and Nielsen 1992). The Sr:Ca ratios were measured in a minimum of four points adjacent to primordia and in an equal number of points along a transect in the first summer of growth. A fish was determined to be of steelhead maternal origin if the mean Sr:Ca ratio of the primordia associated points (hereafter referred to as core region) was significantly higher than that in the first-summer growth region based on an unpaired one-tailed *t*-test with $\alpha = 0.05$. Based on these results, each fish was classified as the progeny of a steelhead or rainbow trout female parent.

After the determination of maternal origin, the slides were polished to remove the carbon coat. Migratory history (anadromous or nonanadromous) was determined for each fish by measuring the Sr:Ca ratio along a standard axis from the center of the otolith core to the edge of the otolith using a laser ablation system (New Wave, 213 nm) coupled to an Agilent 7500c, quadropole, inductively coupled, plasma mass spectrometer (LA–ICPMS) following the methods of Arai et al. (2007) and Brenkman et al. (2007). Laser transects were conducted at a pulse rate of 10 Hz and a beam diameter of 30 μm and run as a continuous scan from core to edge. Calibration was conducted using standardized reference materials (NIST 612). Calcium was used as an internal standard. Core-to-edge transects of the Sr:Ca ratio were visually examined for significant increases in otolith Sr:Ca indicating migration to higher-salinity environments.

Water chemistry.—Because some freshwaters are high in ambient strontium, it is important to confirm water chemistry of locations where otoliths are collected (Rieman et al. 1994; Zimmerman 2005). Water samples were collected from a central location within each stream reach where otoliths were collected in March, July, and November in 2003, 2004, and 2005. Calcium and strontium were analyzed using standard methods SM311B and SM3113, respectively (APHA et al. 1992). Mean elemental concentrations and molar ratios of Sr:Ca were calculated to characterize water chemistry at each location.

Results

Maternal Origin and Migratory History

A total of 964 otoliths were examined to determine age, maternal origin, and migratory history. Age-0 fish were collected from only three sites: Deer Creek, Yuba River, and Calaveras River (Table 1). Age composition of samples analyzed varied among locations (Table 1). Similarly, length composition of fish analyzed varied among locations (Table 1; Figure 2). Mean length at age varied among locations (Table 1).

Mean ± SD otolith Sr:Ca ratios (reported as atomic ratios) in the first-summer growth region (freshwater growth region) ranged from 0.0005 ± 0.0002 to 0.0016 ± 0.0002 among sites. Mean otolith Sr:Ca ratios in freshwater growth regions were positively

TABLE 1.—Mean ± SD fork length (mm; sample sizes in parentheses) of steelhead and rainbow trout collected from Central Valley rivers for otolith analysis between 2001 and 2007.

Location	Age-class				
	0	1	2	3	≥4
Sacramento River		216 ± 12 (8)	294 ± 34 (12)	367 ± 21 (32)	488 ± 52 (102)
Deer Creek	81 ± 8 (49)	142 ± 28 (74)	208 ± 15 (30)	297 ± 28 (2)	
Yuba River	68 ± 24 (26)	228 ± 2 (5)	271 ± 24 (27)	348 ± 25 (40)	424 ± 29 (43)
Calaveras River	115 ± 22 (16)	190 ± 9 (29)	251 ± 28 (84)	335 ± 29 (43)	479 ± 104 (8)
San Joaquin River			238 ± 37 (6)		
Stanislaus River		175 ± 20 (18)	253 ± 28 (77)	342 ± 27 (47)	474 ± 74 (15)
Tuolumne River		178 ± 14 (37)	251 ± 36 (36)	356 ± 23 (36)	444 ± 36 (38)
Merced River			235 ± 25 (5)	348 ± 25 (5)	520 ± 99 (13)

correlated with ambient water Sr:Ca ratios ($r^2 = 0.75$, $n = 7$, $P = 0.01$; Figure 3). Mean otolith Sr:Ca in the freshwater growth regions, however, was weakly correlated with mean ambient water Sr concentrations ($r^2 = 0.11$, $n = 7$) indicating that it is the Sr:Ca ratio of the water, rather than Sr concentration, that controls otolith Sr:Ca ratios. Because only six fish were collected in the San Joaquin River, it was excluded from this regression.

Mean otolith Sr:Ca ratios in core regions ranged from 0.0003 ± 0.0003 to 0.0024 ± 0.0001. The difference between core and freshwater-growth-region Sr:Ca ratios were of a bimodal distribution with modes corresponding to assigned maternal origin (Figure 4). Of the 964 otoliths examined, 224 were classified as steelhead progeny and 740 were classified as progeny of rainbow trout females. The proportion of steelhead progeny ranged from 0.04 in the Merced River to 0.74 in Deer Creek (Figure 5). Of the six juvenile fish captured in the San Joaquin River at Mossdale, presumed to be steelhead smolts based on location and date of capture, coloration, and size, two fish were classified as having a maternal origin of steelhead, while four fish were of rainbow trout maternal origin.

Otolith Sr:Ca ratios along the transects of otoliths from 959 fish were low across the entire transect and consistent with patterns expected for rainbow trout (Figure 6). Five fish were characterized by increased Sr:Ca ratios in the older otolith growth regions indicating migration to high Sr:Ca ratio (presumably marine) environments (Figure 7) and were classified as steelhead. The fork lengths of these steelhead ranged from 455 to 700 mm and all steelhead were age 4 or older. Two adult steelhead were detected in the Calaveras River (535 and 700 mm), and one steelhead was detected in the Sacramento River (460 mm), Stanislaus River (690 mm), and Tuolumne River (455 mm). Three rainbow trout greater than 600 mm were collected in the Merced River, but none of these were characterized by increased otolith Sr:Ca ratios indicating that they had not migrated to saltwater. Similarly, eight fish of 570–600 mm were captured in the Sacramento River and were all classified as rainbow trout. Two fish were classified as "unknown" migratory history because otolith transects were measured through vateritic regions and a reliable migratory history could not be determined (Brown and Severin 1999).

Water Chemistry

Mean Sr concentrations at all sites were less than 1 mg/L, and mean Ca concentrations ranged from 4.54 to 33.58 mg/L (Table 2). The Sr:Ca ratios of ambient stream water ranged from 2.1 to 8.1 mmol/mol among the sampling sites and dates and mean Sr:Ca ratios ranged from 2.88 to 6.74 mmol/mol (Table 2). San Joaquin River was characterized by Sr:Ca ratios ranging from 5.5 to 8.1 mmol/mol, which are approaching values observed in marine waters, which range from 8.6 to 8.74 mmol/mol (Bruland 1983; Nozaki 1997). Donohoe et al. (2008) determined that discrimination of steelhead versus rainbow trout progeny using otolith Sr:Ca core values is appropriate in streams with water Sr:Ca ratios less than 5 mmol/mol but limited at higher values. Using this criterion, water chemistry among all locations, with the exception of the San Joaquin River, are low enough to allow discrimination of maternal origin.

Discussion

We detected steelhead progeny in all of the Central Valley streams examined, and simply documenting the occurrence of steelhead progeny in some of these sites is significant. Owing to limited monitoring of steelhead in Central Valley streams, there is little information concerning the distribution of steelhead spawning. These results begin to address this gap in our knowledge of steelhead distribution and life history within the Central Valley. Because otolith-based analyses are lethal, we were unable to collect sufficient

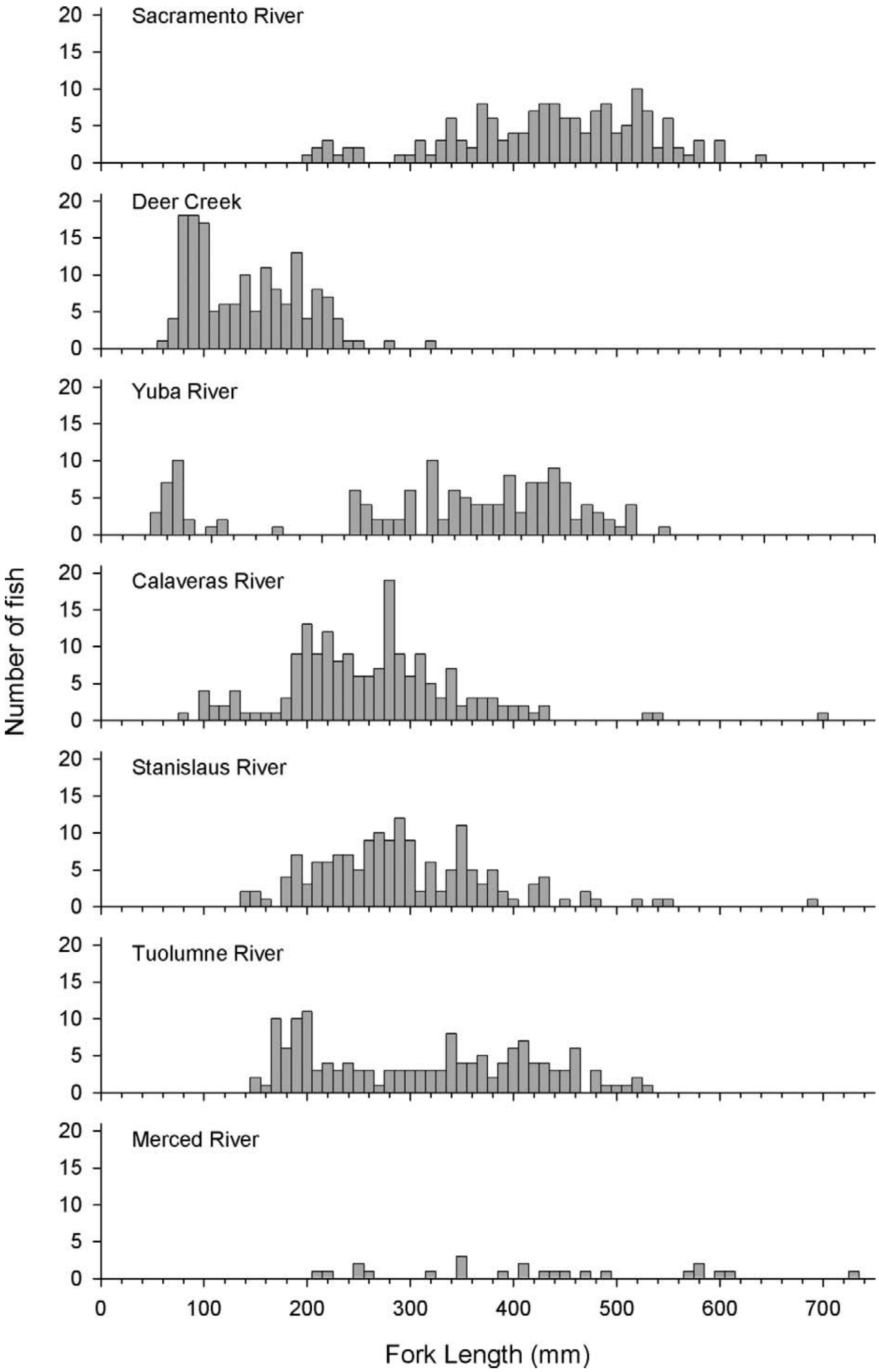

FIGURE 2.—Frequency distributions of the fork lengths of steelhead and rainbow trout collected from Central Valley rivers for otolith analysis.

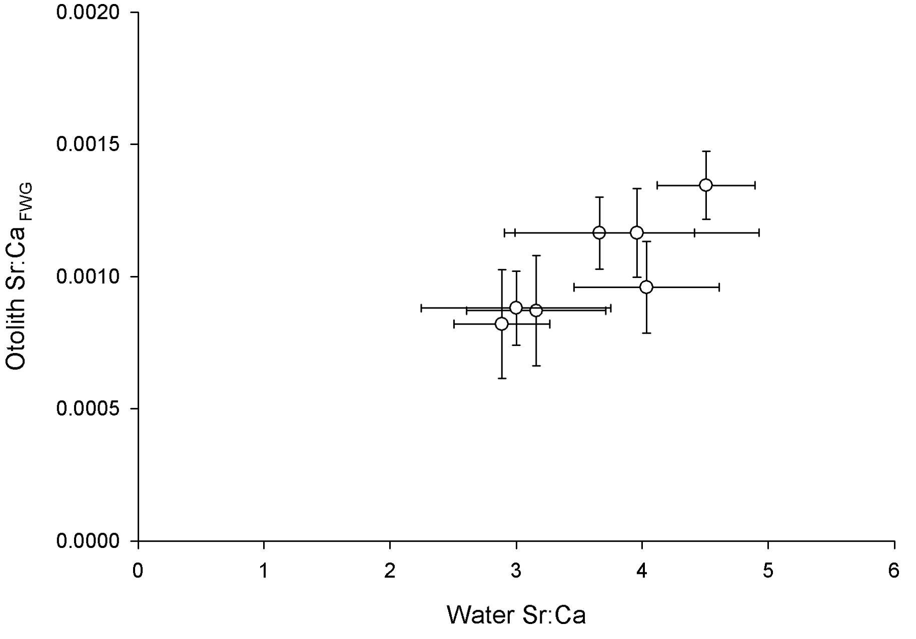

FIGURE 3.—Relationships between the Sr:Ca ratios (mmol/mol) in water and those in the freshwater growth regions of steelhead and rainbow trout collected from Central Valley rivers. The circles represent means and the error bars SDs.

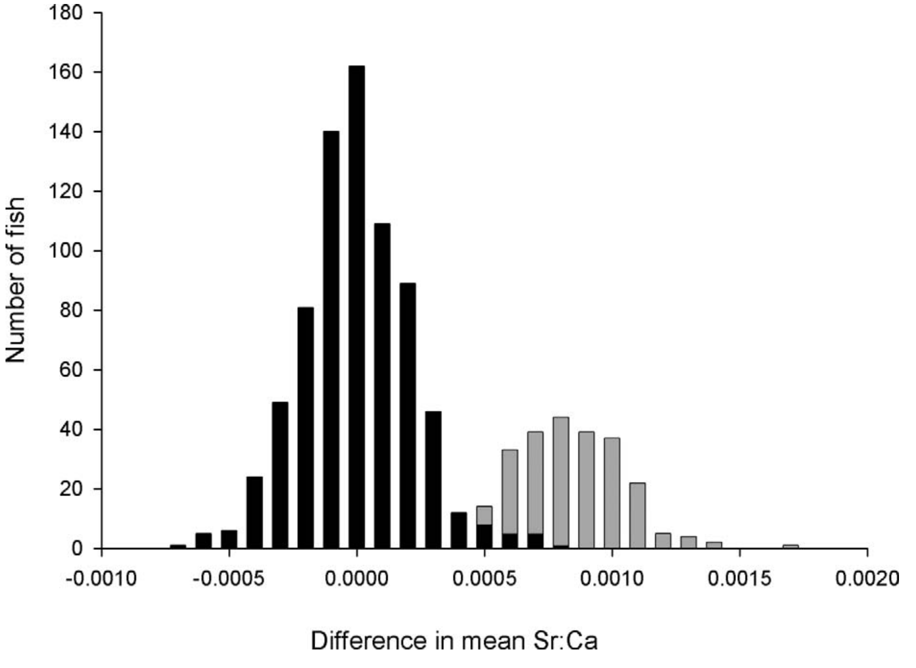

FIGURE 4.—Frequency distribution of the differences between the mean core Sr:Ca ratio and the mean Sr:Ca ratio in the freshwater growth region for 964 steelhead and rainbow trout captured in Central Valley rivers between 2001 and 2007. Black bars represent fish classified as rainbow trout progeny, gray bars fish classified as steelhead progeny.

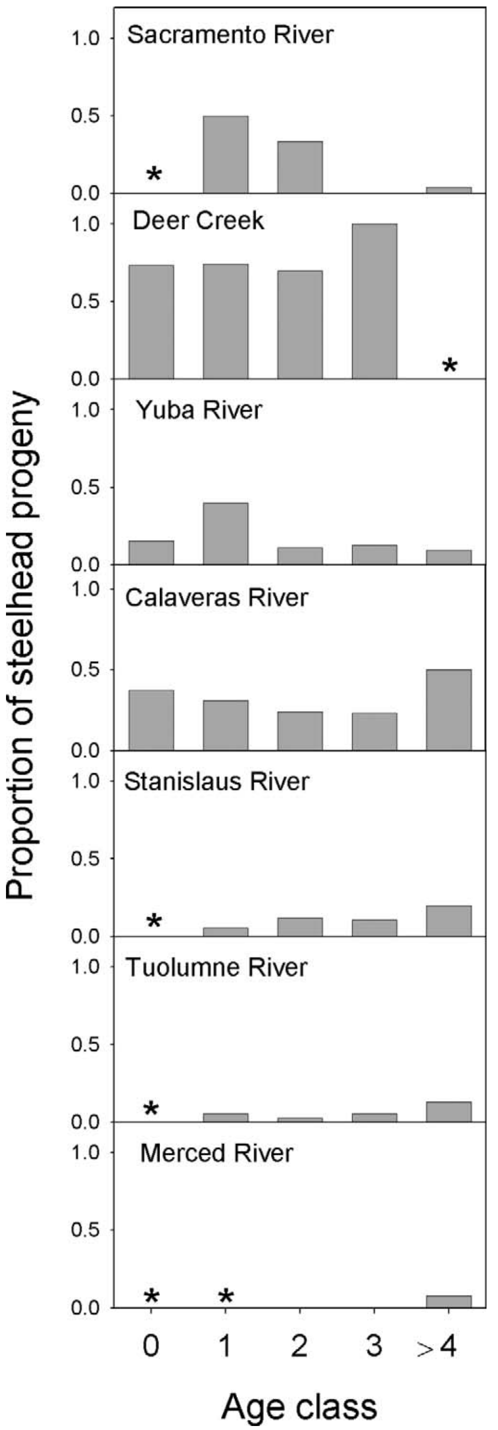

FIGURE 5.—Proportion of steelhead and rainbow trout of steelhead maternal origin by age-class in rivers of the Central Valley. Age-class 4 includes fish of age 4 and above; asterisks indicate that there were no fish in a particular age-class.

samples to determine the actual contribution of steelhead and rainbow trout progeny at these sites at any single point in time.

Our estimates of steelhead occurrence should be viewed as conservative. For example, the fish classified as rainbow trout of maternal origin that fall in the upper mode of Figure 4 were classified as rainbow trout because the difference in mean core and freshwater-growth-region Sr:Ca ratios was not significantly different even though it was high. There are two reasons that fish could have been misclassified. First, if ambient water conditions are high in Sr:Ca ratio, nonmigratory rainbow trout would have Sr:Ca ratios in the core that would be indistinguishable from steelhead progeny. To confirm this was not the case, we sampled ambient water to ensure we could distinguish the two forms. Secondly, dilution of core Sr:Ca ratios has been observed in steelhead that make long freshwater migrations or overwinter in freshwaters before spawning (Volk et al. 2000; Donohoe et al. 2008). Presumably, winter steelhead (the form found in Central Valley streams) do not remain sufficiently long in freshwater to result in significant dilution, but Donohoe et al. (2008) found evidence of such dilution effects when coupled with higher ambient Sr:Ca ratios in some streams. Donohoe et al. (2008), therefore, suggested that determination of maternal origin should be limited to fish coming from streams with Sr:Ca ratios less than 5.5 mmol/mol. All tributary sites we examined were below this value (Table 2). Donohoe et al. (2008) provide a model approach to use in place of methods used by Zimmerman and Reeves (2002). Zimmerman and Reeves (2002) used *t*-tests to compare mean Sr:Ca ratios in primordia with those in the freshwater growth region (as we did in this study); if mean primordia values were significantly higher than mean freshwater-growth-region values, the fish was classified as the progeny of an anadromous female. The method presented by Donohoe et al. (2008) uses core Sr:Ca values, migration difficulty index (elevation × distance from ocean), and ambient water Sr:Ca ratios to distinguish progeny of anadromous and nonanadromous rainbow trout. We used the equations provided by Donohoe et al. (2008) to calculate predicted otolith core Sr:Ca ratios for resident and anadromous progeny in our study sites. Observed mean core Sr:Ca ratios for progeny classified as resident and anadromous were similar to those predicted by the Donohoe et al. (2008) model indicating that both methods are appropriate for assessing maternal origin for fish from these streams (Figure 8). Deer Creek, however, stands out as an outlier with greater observed mean core Sr:Ca ratios than predicted using the Donohoe et al. (2008) models. Given the distance and elevation of Deer Creek, the

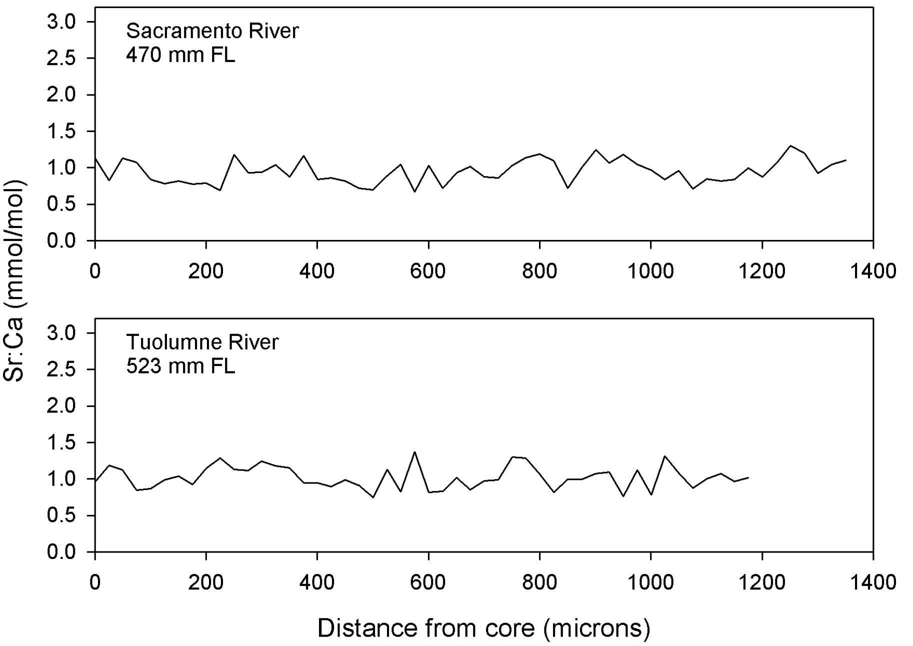

FIGURE 6.—Representative transects of otolith Sr:Ca ratios for fish classified as resident rainbow trout from two Central Valley rivers.

Donohoe et al. (2008) model predicts that we should be unable to use core Sr:Ca ratios to discriminate anadromous and nonanadromous progeny. It is unclear why this population stands out with greater core Sr:Ca ratios than predicted.

The otoliths collected from juvenile rainbow trout in the San Joaquin River at Mossdale (location 5 in Figure 1) were presumed to be from steelhead smolts based on coloration but turned out to be from fish of both steelhead and rainbow trout maternal origin, suggesting that rainbow trout can produce smolts in the Central Valley. With such a small sample size we are unable to draw conclusions about the contribution of progeny of rainbow trout females to the emigration of smolts. Similarly, in presumed steelhead smolts collected in an estuary of a small central California coastal stream (Pilarcitos Creek at Half Moon Bay), juveniles of both steelhead and rainbow trout maternal origin were present (C. E. Zimmerman, unpublished data). Further work is needed to assess the contribution of rainbow trout progeny as smolts and the fate of these fish compared with smolts of steelhead maternal origin.

Our results do suggest that the proportional occurrence of steelhead progeny may vary among locations. Deer Creek, for example, is dominated by steelhead progeny while the Tuolumne and Stanislaus rivers were dominated by rainbow trout progeny. In the Sacramento River, progeny of steelhead were present in samples of age-1 and age-2 fish, but rare in age-3 and older samples. Since steelhead in the Sacramento River predominately smolt at age 2 (Hallock 1989), it is likely that the reduction in the occurrence of steelhead progeny in older ages is a result of smolt emigration.

Further work is needed to better assess the contribution of steelhead and rainbow trout to the anadromous population of *O. mykiss* in streams throughout the Central Valley. Tagging studies of smolts and pedigree studies such as those described by Seamons et al. (2004) and suggested by Hendry et al. (2004) could provide an opportunity to address the relationship of steelhead and rainbow trout and the role of environmental variables in controlling life history. Studies of this sort could use hypervariable microsatellite markers to assess lifetime reproductive success of individuals that adopt different life histories (steelhead versus rainbow trout) across a range of stream conditions and individual characteristics such as growth, size, energy density, and age (Hendry et al. 2004). Although studies of this type would be difficult and costly, they offer the promise of better understanding the relationship of anadromous and nonanadromous life history forms as requested by Lindley et al. (2007). Paired studies built upon existing monitoring efforts across the range of environmental conditions observed in Central Valley streams (such as Deer

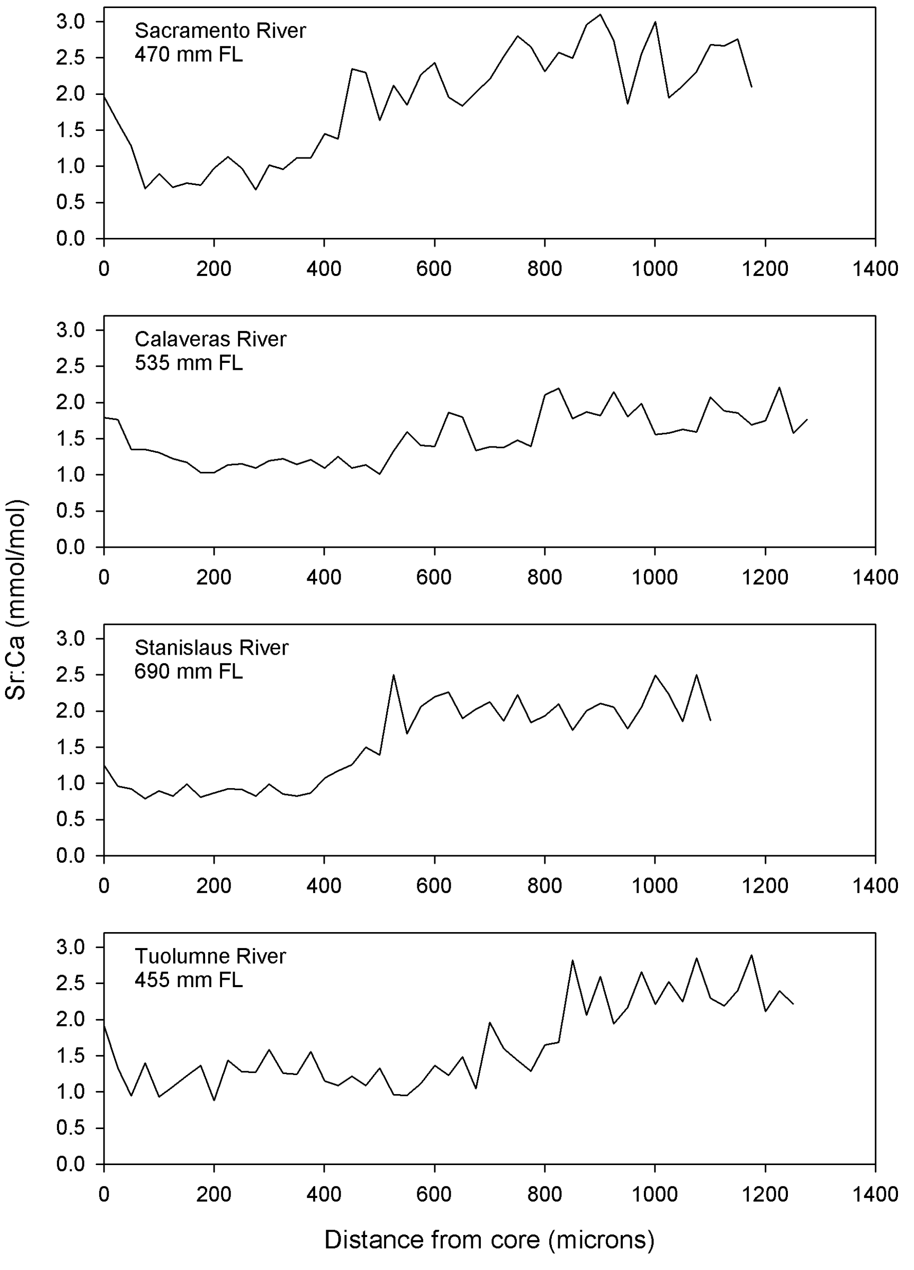

FIGURE 7.—Representative transects of otolith Sr:Ca ratios for fish classified as anadromous rainbow trout (steelhead) from four Central Valley rivers.

Creek and the Stanislaus River) provide ample opportunity for studies of this type.

Acknowledgments

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TABLE 2.—Elevation, distance from the Golden Gate (entrance to San Francisco Bay), mean ± SD Ca concentration, mean ± SD Sr concentration, and Sr:Ca ratio of sampling sites in Central Valley rivers. Water samples were collected in March, July, and November of 2003, 2004, and 2005; $n = 9$ for each site. Site numbers correspond to those in Figure 1.

Site	Location	Elevation (m)	Distance (km)	Ca (mg/L)	Sr (μg/L)	Sr:Ca (mmol/mol)
1	Sacramento River	115	550	13.5 ± 4.0	91 ± 43	3.00 ± 0.75
2	Deer Creek	606	499	9.1 ± 0.9	73 ± 18	3.66 ± 0.75
3	Yuba River	61	301	9.8 ± 0.8	62 ± 11	2.89 ± 0.38
4	Calaveras River	76	217	20.5 ± 3.3	140 ± 22	3.16 ± 0.55
5	San Joaquin River	4	186	33.6 ± 12.8	503 ± 204	6.74 ± 1.11
6	Stanislaus River	98	310	7.6 ± 1.5	74 ± 15	4.51 ± 0.39
7	Tuolumne River	55	317	4.5 ± 0.9	39 ± 12	3.96 ± 0.97
8	Merced River	91	366	5.6 ± 3.2	48 ± 25	4.03 ± 0.57

Jeff Kozlowski from Jones and Stokes Associates. Thor Tingey, Shiway Wang, Dona Eidam, and Vanessa von Biela prepared and cataloged all the otoliths analyzed in this study. Matt Keyse, Tristan Wagner, and Nate Bickford conducted the LA–ICPMS analyses at the University of Alaska–Fairbanks. John Seigle and Robert Oscarson assisted with electron microprobe analyses. Analysis of water chemistry was performed under the direction of Dave Crane at the CDFG Fish and Wildlife Water Pollution Control Laboratory. We thank Dennis McEwan, Robert Titus, and John Seigle for input and advice concerning this study. Funding for this study was provided by the USFWS Anadromous Fish Restoration Program, CDFG, and the U.S. Geological Survey. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

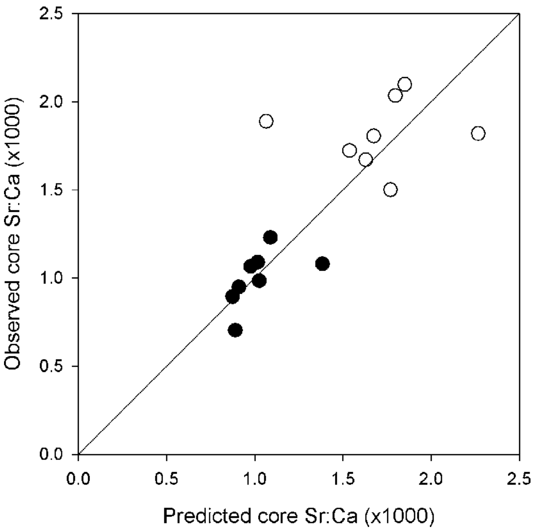

FIGURE 8.—Predicted otolith core Sr:Ca ratios using the Donohoe et al. (2008) model versus mean Sr:Ca ratios observed in fish classified as resident rainbow trout (solid circles) and anadromous rainbow trout (open circles) progeny from Central Valley rivers. The 45° line represents a 1:1 relationship.

References

APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation. 1992. Standard methods for the examination of water and wastewater, 18th edition. APHA, Washington, D.C.

Arai, T., T. Hirata, and Y. Takagi. 2007. Application of laser ablation ICPMS to trace the environmental history of chum salmon *Oncorhynchus keta*. Marine Environmental Research 63:55–66.

Brenkman, S. J., S. C. Corbett, and E. C. Volk. 2007. Use of otolith chemistry and radiotelemetry to determine age-specific patterns of anadromous bull trout in the Hoh River, Washington. Transactions of the American Fisheries Society 136:1–11.

Brown, R. J., and K. E. Severin. 1999. Elemental distribution within polymorphic inconnu (*Stenodus leucichthys*) otoliths is affected by crystal structure. Canadian Journal of Fisheries and Aquatic Sciences 56:1898–1903.

Bruland, K. 1983. Trace elements in seawater. Pages 157–220 *in* J. P. Riley and R. Chester, editors. Chemical oceanography, volume 8. Academic Press, London.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, K. Neely, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

Donohoe, C. J., P. B. Adams, and C. F. Royer. 2008. Influence of water chemistry and migratory distance on ability to distinguish progeny of sympatric resident and anadromous rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 65:1060–1075.

Foote, C. J., C. C. Wood, and R. E. Withler. 1989. Biochemical genetic comparison of sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 46:149–158.

Hallock, R. J. 1989. Upper Sacramento River steelhead (*Oncorhynchus mykiss*), 1952–1988. Report to the Fish and Wildlife Service, Sacramento, California.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. Berg. 2004. To sea or not to sea? Anadromy versus nonanadromy in salmonids. Pages 93–125 *in* A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, New York.

Howland, K. L., W. M. Tonn, J. A. Babaluk, and R. F. Tallman. 2001. Identification of freshwater and anadromous inconnu in the Mackenzie River system by analysis of otolith strontium. Transactions of the American Fisheries Society 130:725–741.

Kalish, J. M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and nonanadromous salmonids. U.S. National Marine Fisheries Service Fishery Bulletin 88:657–666.

Kalish, J. M., R. J. Beamish, E. B. Brothers, J. M. Casselman, R. I. C. C. Francis, H. Mosegaard, J. Panfili, E. D. Prince, R. E. Thresher, C. A. Wilson, and P. J. Wright. 1995. Glossary for otolith studies. Pages 723–729 *in* D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. Belle W. Baruch Library of Marine Science, Columbia, South Carolina.

Lindley, S. T., R. S. Schick, B. May, J. J. Anderson, S. Greene, C. Hanson, A. Low, D. McEwan, R. B. MacFarlane, C. Swanson, and J. G. Williams. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. San Francisco Estuary and Watershed Science [online serial] 4(1): article 2.

Lindley, S. T., R. S. Schick, E. Mora, P. B. Adams, J. J. Anderson, S. Greene, C. Hanson, B. P. May, D. R. McEwan, R. B. MacFarlane, C. Swanson, and J. G. Williams. 2007. Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento–San Joaquin basin. San Francisco Estuary and Watershed Science [online serial] 5(1): article 4.

McEwan, D. R. 2001. Central Valley steelhead. California Department of Fish and Game, Fish Bulletin 179.

Narum, S. R., C. Contor, A. Talbot, and M. S. Powell. 2004. Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, USA. Journal of Fish Biology 65:471–488.

Neave, F. 1944. Racial characteristics and migratory habits in *Salmo gairdneri*. Journal of the Fishery Research Board of Canada 6:245–251.

Nozaki, Y. 1997. A fresh look at element distribution in the North Pacific. EOS 78:221–223.

Pascual, M. A., P. Bentzen, C. M. Riva Rossi, G. Mackey, M. Kinnison, and R. Walker. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Transactions of the American Fisheries Society 130:53–67.

Rieman, B. E., D. L. Myers, and R. L. Nielsen. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. Canadian Journal of Fisheries and Aquatic Sciences 51:68–77.

Seamons, T. R., P. Bentzen, and T. P. Quinn. 2004. The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. Environmental Biology of Fishes 69:333–344.

Secor, D. H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. U.S. National Marine Fisheries Service Fishery Bulletin 90:798–806.

Toole, C. L., and R. L. Nielsen. 1992. Effects of microprobe precision on hypotheses related to otolith Sr:Ca ratios. U.S. National Marine Fisheries Service Fishery Bulletin 90:421–427.

Volk, E. C., A. Blakley, S. L. Schroder, and S. M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using core chemistry to distinguish maternal associations with sea and freshwaters. Fisheries Research 46:251–266.

Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2000. Chinook salmon in the California Central Valley: an assessment. Fisheries 25(2):6–20.

Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:88–97.

Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152–2162.

Zimmerman, C. E., and G. H. Reeves. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 131:986–993.

Zimmerman, C. E., and R. L. Nielsen. 2003. Effect of analytical conditions in wavelength dispersive electron microprobe analysis on the measurement of strontium-to-calcium (Sr/Ca) ratios in otoliths of anadromous salmonids. U.S. National Marine Fisheries Service Fishery Bulletin 101:712–718.

Zimmerman, C. E., R. W. Stonecypher, and M. C. Hayes. 2003. Migration of precocious male hatchery Chinook salmon in the Umatilla River, Oregon. North American Journal of Fisheries Management 23:1007–1015.